ORGANIC RESPONSE[1]

Recent events in the field of evolution comprehend a number of movements and accomplishments of extraordinary interest. The rediscovery of the facts of alternative inheritance, the formulation of the concepts of equivalent, balanced, paired or differential characters, the results of statistical studies of variability, the analyses of species of various constitution by pedigree cultures, in which the value of fertilization from various sources is carefully measured, the distinction of the biotype or genotype as a hereditary entity, the recognition of the possibilities in the action of pure lines within a specific group, the cytological contributions of fact and forecast upon the physical aspects of heredity, and lastly the presentation of the facts and allowable generalizations identified with the mutation theory, comprise a series of advances, of accretions to knowledge, furnish a broadened foundation for biological science and disclose additional possibilities in all lines of experimental research with living things, besides opening up new realms for speculative thought and stimulating the scientific imagination to renewed fruitfulness.

The pressure of undisciplined evidence bearing upon almost all phases of evolution has awakened a freshened chorus of voices crying the virtues of special interests and extolling the sufficiency of theories dignified by age and more or less weighty with authority. Those busy with vitalism of various patterns have spun a moiety to mend the breaks in the fragile web of their gossamer tissue made by the impact of new facts. Isolation and geographical distribution have again been elaborated to account for all differentiation and what their exponents are pleased to term speciation. The anticipatory formation of structures in a rudimentary condition with a long prefunctional progress, guided by the morphological possibilities and actuated by internal impulses, has again been offered to us, fortified by some facts and much clever logic, in such manner as to avoid most of the serious objections offered, except those of physiological morphology.

Natural selection with diverse meanings and manifold implications, has been made to explain development, differentiation and general evolutionary progress, and the tumult is still great about the idea of mutation. Undeniable occurrences of saltatory changes in hereditary lines are numerous and well known, yet it is probable that the importance of mutation as a general procedure varies in different groups of organisms and certain that many shades of opinion as to its exact part in the evolution of living things will always be held.

The situation with regard to the theory which predicates direct adjustment of the organism, quickly or slowly, as the case may be, to environic factors, and the full inheritance of the alterations constituting such variations is far more serious. The various corollaries of this theory have the force of a certain obviousness, its assumptions have been of ready service to the systematist and biogeographer, and its conclusions have long been tolerated in the absence of decisive tests which are not to be easily made or readily carried out. The time has now arrived, however, when the claimants for Neo-Lamarckianism and all of its conclusions must show cause for its further consideration, or else allow it to drop from the position of being seriously taken as a possible method of evolutionary advance. That no subject is the center of a wider interest is amply demonstrated by

[1] Abstract of presidential address, Society of American Naturalists, Ithaca, New York, December 29, 1910. For full text see *American Naturalist* for January, 1911.

the numbers of recent contributions which may be cited. The positive advance implied is so marked as to justify this discussion within two years of the time when the entire matter was presented comprehensively in connection with the various Darwin anniversary programs.

It is unanimously agreed that organisms, plants as well as animals, change individually in aspect, in form and structure of organs, in functionation and habit as they encounter swamps, saline areas, gravelly uplands or slopes, climatic differences identifiable with latitude or elevation, and other physical and biological factors. It is assumed that these somatic alterations are accommodative and adaptive, making the organism more suitable for the conditions which produce the changes. Such an assumption is an over-reaching one. Any analysis of the changes which an organism undergoes after transportation to a new habitat will disclose one, or a few alterations which might be of advantage in dealing with the newly encountered conditions, but with these are many others, direct, necessitous, atrophic or hypertrophic as to organs which have no relation whatever to usefulness or fitness. Further, a critical examination fails to disclose any theoretical considerations or any actual facts which would connect inevitably the somatic response with the nature of the excitation, outside of the specialized tropisms in which specific reactions are displayed. Even in these the adjustment is of such nature that a mechanism specially responsive to contact, tendrils, for example, responds in the same manner to temperature variations, to which the movements are in no sense accommodations or adjustments.

With regard to the more obvious and direct responses of organisms to altered environment, the records of the operations of the horticulturist, the agriculturist and the breeder as to the behavior of crops, plants and domestic animals, when transferred from one habitat to another, are rich in information. The greater part of such data is the result of observations which do not comply with the ordinary requirements in the avoidance of error so that strict comparisons as to the behavior of organisms under the conditions of various habitats are impossible, but the literature yields many suggestions for experimental research, and the simple generalization that the direct effects of climatic complexes on the seasonal cycle, and upon color, or structural features of the individual, may be repeated or carried over two or three generations, in a habitat where the specific causal combinations are lacking.

Although organized with due regard to the requirements of strict experimentation, the lowland and alpine cultures of plants by Nägeli and Bonnier offer us nothing more decisive than the above. Likewise many experiments dealing with the responses of organisms to selected agencies have obtained nothing but negative results, even when artificial selection was employed to accentuate or perpetuate the feature constituting the reaction.

Buchanan working with *Streptococcus lacticus* finds that phases of fluctuating variations of certain features induced by external exciting agencies may not be fixed and are not transmissible. Jennings' cultures of paramœcia were carried through hundreds of generations with no progressive action in fluctuating variability, while the organism, as a whole, was strongly resistant to all kinds of environic influences: actual alterations were extremely rare. Most of the supposedly acquired characters disappeared in two or three generations by fission.

In the experiments of Sumner mice reared in a warm room were found to differ con-

siderably from those reared in a cold room in the mean length of the tail, foot and ear, and the differences were transmitted to the next generation. The differences may be reasonably designated as being directly individual and somatic, and as having been transmitted by the germ-plasm, which was not subject to the action of various temperatures in the first instance. The reaction forms have an additional claim upon our attention, since they are the ones which distinguish northern and southern races of many animals. The crucial test of the value of the alterations induced in the mice is the one applicable to all of the experimentation on this subject, a test in which two parallel series of cultures, one under the altered environment and the other under usual conditions, should be kept going continuously for a longer series of generations, lots being withdrawn from both, from time to time, for continued comparative culture in normal habitat and under other conditions.

The same considerations apply to Kammerer's experiments with salamanders in which the reproductive habits of *Salamandra atra* and *S. maculosa* were altered to resemble each other by specialized exposure to climatic factors, and while his later work with *Lacerta* has resulted in the production of some extremely striking changes in the color bands which behaved in a Mendelian fashion when paired, yet these have not been followed to the third and fourth generations. The permanency of the induced changes seems highly probable in this case. There is, however, a great body of properly authenticated evidence which demonstrates conclusively that external agencies acting upon bacteria, crustaceans, beetles, fungi and some of the higher types of seed-plants have been seen to result in the appearance of new types or genotypes, which have been found to transmit their characters perfectly through so many generations as to indicate practical permanency.

The names of Beijerinck, Winogradsky, Lepeschkin, Hansen and Barber are associated with records of mutational occurrences in pedigreed strains of yeasts and bacteria under pressure of unusual media or other environic conditions. Some aberrants being propagated by fission and others through the spore stage, some only by selection and others independently. In addition Pringsheim finds many accommodative responses to unusual culture media, temperatures and poisons, which may be cumulated and become fixed in these lower organisms, being transmissible by fission or by spores.

My own earlier work with relation to this subject consisted chiefly of ovarial treatments in which the main and accessory reproductive elements of seed-plants were subjected to the direct action of solutions of various kinds. A new combination of characters constituting a distinct elementary species or genotype was obtained in one plant, and the divergent type has been found to transmit its qualities in the fullest degree, as far as tested, to the fifth generation. Still more marked forms were obtained in a second genus, the divergent progeny being lost in transference to the Desert Laboratory, while distinct responses have been obtained in the extensions of these experiments upon species representing widely different morphological types in Arizona. The greater majority of the tests have been made upon plants growing under natural conditions, so that environmental reaction in addition to that of the specific reagents might be excluded. Progenies representing many species, including thousands of individuals, many of which are divergents, are now under observation. Absolute finality of decision with respect

to the standing of the new types may be reached but slowly.

The important results of Tower, in which new types and various hereditary departures in the Leptinotarsæ were induced by the action of climatic factors on the germplasm, have been so fully described and repeatedly cited that any further description is unnecessary at the present time.

Gager produced chromosomic irregularities by the exposure of ovaries of *Œnothera* to radium emanations a few years ago and some of the progeny from treated parents were aberrant, but the transmissibility of the new characters was not tested. By the use of similar excitations Morgan has recently induced the appearance of white eyes and short wings in the fly, *Drosophila,* which characters seem to be fixed and fully transmissible. Both are sex-limited and Mendelize when paired with red eyes and long wings.

Woltereck's cultures of *Daphnia* have yielded some facts of unusual interest in the present connection. The particular group of this crustacean furnishing the experimental material is taken to be very variable, and it was subjected to over-feeding, with the immediate result that the variability of the form of the head appeared to be widened, the size of this structure being increased. This disappeared when lots from the cultures were restored to normal conditions in the earlier stage of the work. After three or four months of over-feeding, the form of the head came within narrower limits, and fewer aberrants were seen, while lots returned to normal conditions, showed a slower restoration of the original form of the head. Two years after the cultures were begun, it was found that the original head form was not displayed by young restored to normal nutrition conditions, the larger helmet being persistent. It seems fairly certain that a new genotype resulted from the long-continued action of the culture medium, which must have influenced the soma and germ-plasm contemporaneously.

Klebs, who has long been concerned with the morphogenic reactions of plants, has determined a series of conditions under which stages of mycelial development, asexual, zoospore and sexual or oospore formations in filamentous fungi may be inhibited or variously interchanged. Much more important reactions were obtained from *Sempervivum,* the live-forever of the garden. In this plant, dense rosettes or propagative bodies are formed at the ends of some branches, and inflorescences were replaced by single flowers by experimental excitation: the number and arrangement of the floral organs as well as of the stamens and carpels could be altered. Furthermore, the deviations in question were found to be transmissible in guarded seed-reproductions.

Lastly we now have the fortunate experiences of Zederbauer with *Capsella* which has yielded some conclusions of exceptional importance. A genotype of *Capsella bursa pastoris* resembling *taraxacifolium* was found on the lower plains of Asia Minor, and displayed the well-known characters of this form, including broad leaves, whitish flowers, and stems 30–40 cm. high. A highway leads to a plateau at an elevation of 2,000 to 2,400 meters, along which the plant has been carried by man, and in this elevated habitat it has taken on certain alpine characters, including elongated roots, xerophytic leaves, stems 2, 5 cm. high, reddish flowers, with a noticeable increase of the hairiness of the entire plant. That the distributional history has been correctly apprehended seems entirely confirmed by the fact that when seeds are taken from the lowlands the

alpine characters enumerated are displayed at once as a direct somatic response. When seeds are taken from plants on the elevated plateau where their ancestors may have been for many years or many centuries (perhaps as long as 2,000 years) and sowed at Vienna, and at other places, it was found that in four generations the leaves lost their xerophytic forms and structure, but the other characters were retained within the limits of variability. The stems showed an increase in average length of 1 to 2 cm., the roots changed as much, but the reproductive branches and floral organs retained their alpine characters. The slight modifications undergone by these features were seen to reach a maximum and to decrease in the latest generations cultivated. The structural changes and implied functional changes are originally direct somatic responses; there is no escape from the conclusions that the impress of the alpine climate on the soma has been communicated to the germ-plasm in such a manner as to be transmissible, and the suggestion lies near that repeated and continued excitation by climatic factors may have been the essential factor in such fixation.

A related phase of the subject is that of the interposition of environic factors in mutations and hybridizations. De Vries appears to have first called attention to the fact that the composition of hybrid progenies of mutants with each other and with the parental form might be altered by nutritive conditions, and the author has described mutants given off by *Œnothera Lamarckiana* in New York which had never been seen in Amsterdam. Furthermore, in discussing the divergent results of De Vries and myself, obtained by crossing the same forms in Amsterdam and New York, the suggestion was made in 1905, that "the manner in which the various qualities in the two parents are grouped in the progeny might be capable of a wide range of variation. Many indications lead to the suggestion that the dominancy and prevalency, latency and recessivity of any character may be more or less influenced by the conditions attendant upon the hybridization; the operative factors might include individual qualities as well as external conditions."

Much more striking evidence upon the matter has been recently obtained by Tower in intercrossing *Leptinotarsa decemlineata, L. multilineata, L. oblongata* and other species in their habitats in southern Mexico, and at the Desert Laboratory. The observations were carried on with both normal and hybrid crosses, in crosses between races which had been built up selectively, and between forms which arose as sports proving conclusively that external agencies may alter the action of paired reproductive elements. Kammerer's contribution to this subject consisted in demonstrating that newly induced color characters in *Lacerta* displayed dominances different from those of the original types, while Tennent has proved that the dominances in crosses of *Hipponoe* and *Toxopneustes* variously attributed to seasonal changes, variations in temperature, etc., are in reality to be attributed to the concentration of the OH ions in the seawater.

The first realization of results of importance from cultures widely extended geographically have been obtained in the experiments with Leptinotarsæ by Tower, in which various species of these beetles were studied in their habitats in southern Mexico, in open air and glass houses as far north as Chicago, as far east as the Atlantic and as far west as the Desert Laboratory. Facilities for work upon special problems are now being organized at sev-

eral places and many contributions to the subject may be expected within the next decade.

The plan for work upon the problems of special interest in connection with the Department of Botanical Research of the Carnegie Institution of Washington, implies the establishment of experimental cultures in localities which furnish distinct types of climate or which have characteristic congeries of meteoric factors, as indicated by the vegetation indigenous to them. Secondly, these localities have been chosen with regard to their geographical relations so far as possible, in order that the possible and probable fate of migrating species might be studied. The behavior of plants in these localities is recorded as to anatomical alteration and physiological departure. Having detected some such feature of apparent importance, its reappearance in plants from seeds carried to the original habitat and other locations is followed as one line of evaluation. Contemporaneously, the form is taken into the laboratory and here by analytical experimental tests the effort is made to ascertain to what special agencies the departures are due. Such determination of the identity of exciting agencies has been made by Stockard, who found that the cyclopean embryos of *Fundulus* occurring in nature could be induced by the action of magnesium salts introduced into the sea-water containing the eggs.

Our increased insight into the nature of natural groups of organisms has shown the necessity and suggested the means of observing certain distinctions and precautions in this work. Thus it is of the greatest importance that the living material shall be shown to be either simple genotypes or that its phænotypic nature be apprehended in order that the integration and combination of these forms shall not be mistaken for environic effects. When a lot of plants is taken from one plantation to another, data of the original locality are preserved, as the stand of the plant in that place serves as the control. If the plant is multiplied vegetatively in the test, it might reveal a possible complex character of the material in bud sports, but other divergencies might be well ascribed to local effects. On the other hand, if introduced in the form of seeds, the possible complex character of the material would soon become apparent, especially if the generations were followed properly. In the actual management of the cultures, it is found profitable to reintroduce forms from the original or control lot of various species in order to follow the first stages of their adjustment repeatedly.

The genetic character of environic effects remains to be considered. In any species or genotype there is, withal, a limited number of things included within the morphological possibilities. The appearance of any character in an acclimatization culture raises a question at once as to the standing of the new feature. Is it a regressive character, once displayed by the species and now recalled, or is it to be considered as a character *de novo*, arising simply and directly in response to the external agencies which have been seen to induce it? Thus our general knowledge of the Cactaceæ leads us to assert with some confidence that the reappearance of a full complement of spines in a prickly pear, from which they had all but disappeared, is a regression or return to the condition of the greater majority of the group, a condition which must have been shared by its ancestors at no remote stage in its progressive development.

None of the attempts hitherto made to perfect a theoretical conception which would be useful in interpreting the mech-

anism of environic responses has had anything more than the most limited usefulness. The stimuli of climatic and many other agencies do not imply the introduction of any strange or new substances into the bodies of the organs affected. These agencies might change the dissociations in such manner as to modify the relative number of free ions and thus alter the molecular complex of the living matter in a very important manner however. The intricate play of enzymatic action might also be altered, and any modification of the relative reaction velocities of the more important processes might result in material and permanent change, especially in those cases, in which external agencies interfere directly with the action of the germ-plasm.

The introduction of solutions into ovaries or the exposure of reproductive elements to unusual irradiation may raise the additional liability of disturbed polarity and of modified surface tensions in the cells. It is conceivable that the rearrangement or disturbance of the localizations of substances, especially the mineral salts, might seriously modify the capacities of the bearers of heredity. These direct and material possibilities offer an adequate basis for the organization of experimental research upon the main subject as well as the means of interpretation of results without recourse to schemes of particulate inheritance or theories as to the constitution of germ-plasm to which may be ascribed usefulness in the discussion of other problems in evolution.

The theoretical considerations which might lead us to assign all cases of perpetuation of environic effects to the direct action of the exciting agency upon the germ-plasm are perfectly competent to be questioned with each new bit of evidence brought forward. My own results so far have been all of this kind, as are many of the instances cited, but the case does not appear so simple when, as in *Sempervivum,* somatic alterations are induced late in the ontogeny and are transmitted by seeds borne on the altered branches, and equally serious doubts are raised when one considers the multifold somatic alterations of *Capsella* and the fact that they must be repeated dozens, perhaps hundreds, of times before being transmissible. One must not lose sight of the fact that the soma is itself the most closely interlocking environment of the germ-plasm, and not until the germ-plasm has been exposed to interaction with a changed soma for repeated generations does it undergo the changes necessary to an altered heredity.

The problems of real interest, however, are those which concern the actual influence of environment upon evolutionary development, and with regard to these many generalizations of importance are becoming possible, and their brief summarization may suggest some encouraging advances.

First it is to be seen that not all environic effects induced in the laboratory or by transplantations are heritable, although they may be carried over for two or three generations. No satisfactory basis has yet been found upon which it might be predicted that any effect would be ephemeral or permanent. The characters induced in an hereditary line may be regressive, or awakened latencies or organizations *de novo.* The alterations which become permanent may be cumulative in construction, although they are mutative or abrupt in their appearance in most instances. Abruptly displayed by some organisms, yet they may not become heritable until the germ-plasm has been repeatedly subjected to the direct action of the exciting agency or to the effect of a changed soma for many generations.

Orthogenetic or heterogenetic as to direc-

tion, they may be consequently accommodative or correlational, incidentally adaptive, or wholly inutile in their functional relations. D. T. MACDOUGAL

EDUCATIONAL AND INDUSTRIAL EFFICIENCY

THE latest bulletin of the Carnegie Foundation has many attractive features. The report has evidently been made up in a spirit of good will to education, and any sting that it may contain should be removed by the admirable introduction by Dr. Pritchett. In the course of more than a hundred and thirty large pages the author, Mr. Cooke, makes a number of excellent suggestions, which are none the less excellent because of their lack of novelty. He is aware that the charge of Philistinism might easily be suggested by the tenor of his remarks and he makes some effort to protect himself accordingly. His peculiar point of view seems to give undue prominence to "the cost per student hour," but although we hear much of this phrase in the report we are distinctly told in one place that "It should be borne in mind that the cost per student-hour has absolutely no value in distinguishing relative educational values." If this had been placed as a headline to all the pages, it would have greatly improved the value of the report, and would have been in harmony with this other admirable sentence which might with equal propriety have been inserted as a foot-note to every page: "In the last analysis the usefulness of a university is the measure of its mental, moral and spiritual product—and product interpreted as broadly as you please."

However, although there is much that is excellent in the report, it has many weaknesses. It is written from the point of view of the man who is used to report on the efficiency of a glue factory or soap works. Whenever it touches the strictly educational field and gets away from the factory the trail of the amateur is over it all. It is full of commonplaces, and there is scarcely a question raised that has not been discussed *ad nauseam* by college professors and other officers. It is not lacking in confidence. One marvels at the temerity even of an "efficiency engineer" who can lay down the law so definitely as to how to teach physics, how to conduct a recitation, how to carry on research, when most of us who have devoted our whole lives to such problems are far less confident. There are, however, here and there some pleasing evidences of diffidence. In discussing the important educational problem of janitor service Mr. Cooke says, "A sharp line should be drawn, *probably,* between the cleaning of the buildings and the care of apparatus." The use of the word "probably" is a master-stroke. It conjures up pleasing pictures of janitors handling the delicate instruments of a physical laboratory just as they furbish the brass plates of a glue factory—if indeed "the snap and vigor of the business administrator" which Mr. Cooke admires so much decree that such things are a necessary adjunct to the dignity of the factory. Almost on a par with this use of "probably" is the statement that "There is a good deal of the feeling that lectures to be good must in a way bear the marks of the inspiration of the moment. But a good many men who have the reputation of being high authorities assured me that the carefully thought out plan for a series of lectures would win out every time over the inspiration of the moment idea." Of course they assured Mr. Cooke of this, but they must have smiled at the naïveté of the question and wondered who ever suggested that the presentation of a scientific subject be left "to the inspiration of the moment."

The report shows many evidences of ignorance of the history of education. It suggests as novelties plans that have been tried for centuries and abandoned only after careful consideration. Such, for example, is the suggestion that the rules for the conduct of the students and the punishments for their breach should be put into precise form. The collection of such rules from the archives of the older universities would fill many volumes. Again he says, "It may turn out that ultimately the matter of examinations will be handled by an agency outside of the depart-